A GENERAL AREA CLADOGRAM FOR MONTANE MEXICO BASED ON DISTRIBUTIONS IN THE PLATYNINE GENERA *ELLIPTOLEUS* AND *CALATHUS* (COLEOPTERA: CARABIDAE)

JAMES K. LIEBHERR

Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999.

Abstract. —Cladistic biogeographic methods are used to derive a general area cladogram for the montane areas of Mexico from the taxon-area relationships exhibited by Mexican taxa in the platynine carabid genera *Elliptoleus* and *Calathus*. Mexican species of both genera are largely restricted to humid montane forest habitats north of the Isthmus of Tehuantepec, and are representative of the Nearctic Distribution Pattern of Halffter. The general area cladogram based on these two groups supports the monophyly of areas in the Sierra Madre del Sur and the Transvolcanic Sierra, with these two major mountain systems together considered the sister group to the Sierra Madre Occidental plus Rocky Mountain cordilleras. The Rio Balsas depression has not been crossed by taxa in either genera during their diversification in Mexico, with faunal exchange likely occurring several times along the Atlantic versant between the Transvolcanic Sierra and Sierra de Oaxaca. The Sierra Madre Oriental exhibits dual affinities; the northern reaches share species across the Chihuahuan desert with the Sierra Madre Occidental, whereas the southern portion supports endemic species with northern affinities and a widespread species also found in the Transvolcanic Sierra. Areas of endemism are smaller in the southern mountains and larger to the north, supporting the greater role of the southern montane regions of the Sierra Madre del Sur and Transvolcanic Sierra in the generation of species-level diversity.

Key Words: Coleoptera, Carabidae, Platynini, *Elliptoleus, Calathus,* biogeography, cladistics, Mexico

The rugged topography of the Mexican mountains supports an incredible array of carabid beetle species, among them many species of the Tribe Platynini. Based on the field collecting of Don Whitehead, George Ball, and subsequent associates, we know that there are more than 300 species assignable to the genus *Platynus* within the borders of Mexico (Whitehead 1973, Liebherr, unpubl. data). This diversity is due both to large numbers of species at any one locality, and to replacement of species across space due to their extremely limited distributions. In many cases, species exhibiting restricted distributions are brachypterous, making long-range dispersal events an extremely unlikely means of colonizing new areas. Based on gut contents, platynine carabids are generalized predators or omnivores, feeding on a variety of terrestrial arthropods. Given their highly endemic distributions, limited dispersal ability, and generalized feeding habits, platynine carabids inhabiting montane regions comprise

a taxonomic group ideal for cladistic biogeographic analysis (Platnick and Nelson 1978, Humphries and Parenti 1986).

I recently completed a taxonomic revision and cladistic analysis of the genus *Elliptoleus*, a genus of 11 species distributed from Arizona and Texas south in the Mexican mountains to the Isthmus of Tehuantepec (Liebherr 1991). That study resulted in a fundamental area cladogram based on *Elliptoleus* distributions. When the data of Ball and Negre (1972) were reanalyzed using cladistic parsimony, the Mexican species of the fellow platynine carabid genus *Calathus* proved to exhibit taxon-area relationships concordant with those observed in *Elliptoleus*. This paper presents the derivation of the fundamental area cladograms for both taxa from their respective taxon-area cladograms, followed by derivation of a general area cladogram for the Mexican montane forest regions inhabited by species of these two genera. This general area cladogram is interpreted in light of geological data and distributional data from a variety of other Mexican montane taxa.

Mexican Montane Biogeographic Patterns

Halffter attempted to distill the vast array of distributional patterns observed in the Mexican montane insect fauna, and categorized them as the Nearctic Distribution Pattern, the Paleo-American Pattern, and the Meso-American Montane Pattern (Halffter 1976, 1987). He considered taxa to represent one of these three patterns based on criteria including overall distribution of the group in question and its near relatives, the amount of sympatry among species, and the diversity of habitats occupied by species of the group.

Halffter considered taxa exhibiting the Nearctic Distribution Pattern to have undergone Pliocene to Pleistocene diversification in the mountains of Mexico. Many possess near relatives (cladistically their sis-

ter group), or member species-level taxa distributed in North America north of Mexico. Their southern limit of distribution is often the Isthmus of Tehuantepec, and if they have species in Central America, such diversity is limited. These taxa occupy habitats that are found above 1700 m elevation; usually temperate conifer forests and high altitude grasslands.

Paleo-American Pattern taxa differ from those representing the Nearctic Pattern principally by exhibiting greater ecological and taxonomic diversity, as well as sister group relationships across Beringia with Old World temperate and tropical groups. These taxa are restricted to the Mexican montane regions, with ecological preferences spanning habitats that include deserts, grasslands, and rain forests. Like Nearctic Pattern taxa, Paleo-American groups may have representative member taxa in Central America.

Halffter's Meso-American Montane Pattern is represented by taxa with a center of diversity in nuclear Central America. They may have South American affinities (cladistically a South American sister group), as well as member taxa in the tropical and cloud forests further north in the mountains of Oaxaca, and further north and west along the Atlantic and Pacific versants. The Meso-American Pattern taxa are hypothesized to have diversified earlier than the Nearctic Pattern taxa, due to their South American affinities and Central American diversification; Halffter hypothesizes their diversification in Central America starting in Oligocene.

Materials and Methods

Taxa.—There are 11 species of *Elliptoleus* (Liebherr 1991), with the aggregate distribution delimited by Texas and Arizona on the north, and the Isthmus of Tehuantepec to the south (Fig. 1). Most species occur in humid temperate forests at 1400 to 3300 m

elevations, exhibiting a high degree of fidelity to the oak-alder-pine forest habitat, with only the northern species *E. acutesculptus* found in drier, more open habitats in the Chihuahuan desert region. I have collected *E. acutesculptus* in pine savannah near Saltillo, Coahuila, where beetles were found only in the shade under the pine trees, indicating that this species prefers cooler, moister situations within its more open habitat. *Elliptoleus acutesculptus* is the only species in the genus for which some individuals possess fully developed metathoracic flight wings; 4 of 63 examined specimens were macropterous, the remainder possessing vestigial wings (Liebherr 1991). All other *Elliptoleus* species are characterized by vestigial flight wings.

Based on Halffter's (1987) classification of biogeographic patterns, *Elliptoleus* exhibits the Nearctic Distribution Pattern. Its sister group is the Holarctic genus *Sericoda* Kirby. Species are restricted to montane forests, and have not diversified ecologically into other habitat types. No species of *Elliptoleus* are found south of the Isthmus of Tehuantepec. Nonetheless, *Elliptoleus* does not exactly fit Halffter's criteria. Based on its sister group relationship with *Sericoda* and diversification patterns within that genus, *Elliptoleus* most likely diversified in Mexico starting in Miocene (Liebherr 1991), not as late as Pliocene to Pleistocene as predicted for Nearctic Pattern taxa by Halffter.

Calathus comprises 20 species in North America north of the Isthmus of Tehuantepec (Ball and Negre 1972). The Mexican species exhibit fidelity to the humid oak-alder-pine forests (Fig. 2) more striking than that exhibited by *Elliptoleus*. Similar to *Elliptoleus*, species of *Calathus* from farther north in Texas are found in more open habitats, but again beetles in these areas tend to cluster under oak trees in such savannah habitats (JKL, unpubl. data), indicating a preference for cooler, moister microhabitats. All Mexican species of *Calathus* are constantly brachypterous, but the six species found in North America north of Mexico—*Calathus advena, C. ruficollis, C. gregarius, C. opaculus, C. calceus,* and *C. ingratus*—vary from constantly to rarely macropterous.

Ball and Negre (1972) considered the diversification of Mexican *Calathus* to have started in Miocene. Given the occurrence of northern taxa in the genus, *Calathus* is also a representative of Halffter's Nearctic Distribution Pattern.

Cladistic biogeographic methods.—The protocol for cladistic biogeography first involves development of a taxon cladogram, which is converted to a taxon-area cladogram by substituting the areas taxa occupy for the taxonomic names of the original cladogram. The taxon-area cladogram is subsequently reduced to a fundamental area cladogram in which each area is represented only once. This reduction may be accomplished using several different sets of conditions, named Assumptions 0, 1, and 2 (Nelson and Platnick 1981, Wiley 1987, Zandee and Roos 1987, Page 1989, 1990). These assumptions determine different methods of analyzing widespread taxa, redundantly represented areas, and areas missing from the distribution of one taxon but represented by another (Humphries and Parenti 1986, Carpenter in press).

How the three sets of assumptions interpret widespread species is most relevant to this analysis. Conversion of a taxon-area cladogram to a fundamental area cladogram is straightforward under conditions of Assumption 0. In this case, widespread taxa are assumed indicative of areas that share a most recent common ancestry. Under Assumption 1, widespread taxa are indicative of taxa that either have not responded to a most recent vicariant event, as assumed under Assumption 0, or to some earlier vicariant events. Assumption 2 is the least restrictive with regard to interpretation of widespread taxa, allowing the conditions under Assumption 1 to prevail, plus the assumption that the species' range may have been determined in part via dispersal subsequent to the origin of the species.
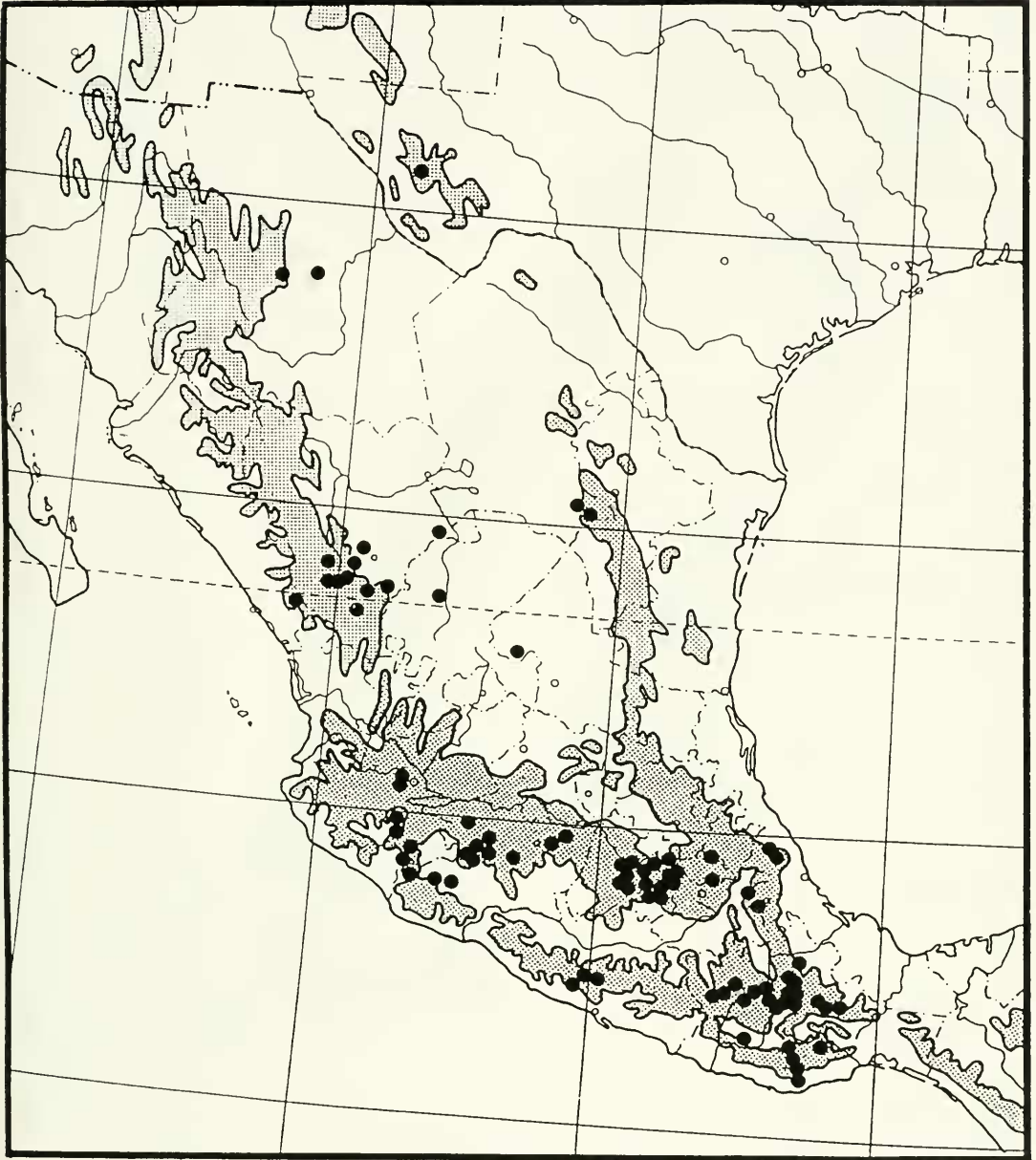
Fig. 1. Distribution of *Elliptoleus* collection records and humid montane forest habitat (stippled) (from Liebherr 1991).

After fundamental area cladograms are determined for all relevant taxa, these cladograms may be compared in order to determine what area relationships, if any, are generally represented. Fundamental area cladograms have been generalized using component analysis (Nelson and Platnick 1981, Page 1989, 1990), overall parsimony of combined data sets (Wiley 1987), and component compatibility (Zandee and Roos 1987).
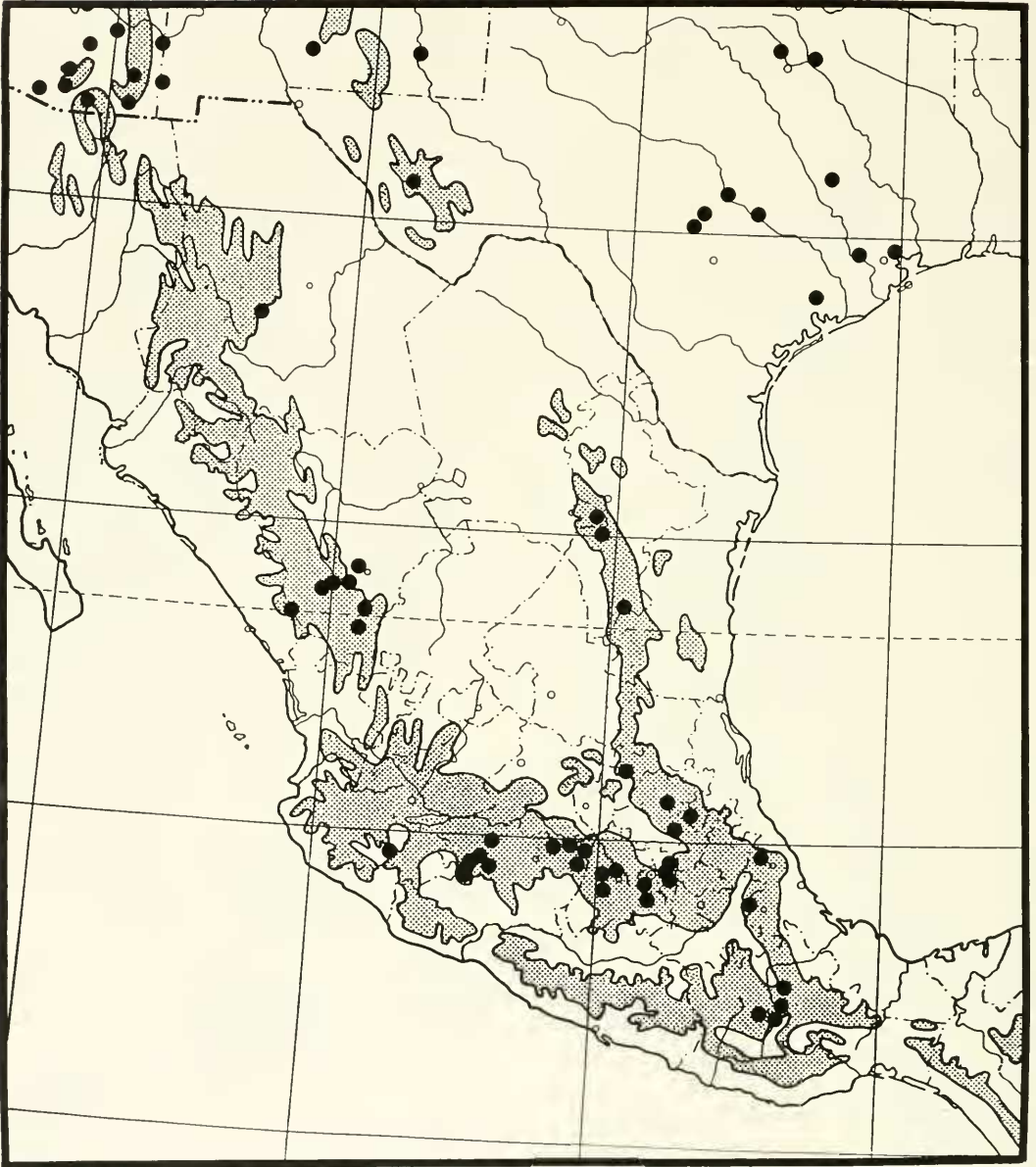
For this analysis, the character data for

Fig. 2.   Distribution of *Calathus* collection records in Mexico and adjoining United States, and humid montane forest habitat (stippled) (data derived from Ball and Negre 1972).

Elliptoleus were taken from Liebherr (1991). As only 11 taxa were represented in the analysis, the most parsimonious taxon cladogram was exactly determined using the exhaustive search option, ie*, of the Hennig86 cladistic computer program (Farris 1988). Hennig86 was also used to deter-mine the most parsimonious cladogram for *Calathus*. In this case, the data presented by Ball and Negre (1972) were modified by removing autapomorphies (characters d, e, j, l, m, and n), followed by coding the re-maining potential synapomorphies as bi-nary or additive binary characters (Kluge

and Farris 1969). The multistate characters that were converted to additive binary characters included character 3, which was recoded as three unit characters, and character 5, which was recoded as two unit characters. The resultant data matrix comprised 14 unit characters for the 20 taxa, and was analyzed using the m* network building, and bb* branch and bound options of Hennig86.

Taxon-area cladograms for both taxa were determined by comparing distributions of all species in both genera, and delimiting areas of endemism by the most restrictive species distributions for any geographic region occupied by a species in either genus. Areas of endemism were defined as: 1) an allopatric species distribution, 2) a region where several congeners are sympatric, or 3) the allopatric remainder of a species range where two species ranges partially overlap. A single species may therefore occupy several areas of endemism determined by its distribution alone, by overlap with one or more other congeners, or by occupation of part of its range by geographically more restricted species in the other genus. This method resulted in areas of endemism that may be defined by the coincident distribution of species, or by the intersection of two incompletely overlapping species ranges. In the former case, the area may be interpreted as a monophyletic entity, diagnosable by the endemic distribution of one or more species. In the latter case, the areas are diagnosable only by the distribution of one species relative to the presence or absence of another; i.e. they are analogous to paraphyletic taxa. Each area of endemism, whether currently interpretable as monophyletic or paraphyletic, has been defined by past speciation events, with subsequent dispersal causing sympatry. Prior to such dispersal, areas currently considered paraphyletic may have been home to an endemic species, i.e. monophyletic. As the analysis commenced without any prior knowledge of area relationships, much less the history

of dispersal of widespread taxa, areas of endemism defined by both criteria were admitted. Accepting both types of areas of endemism allowed concordance of phylogenetic patterns of all taxa, regardless of geographic extent, to determine hypotheses of area relationships.

The taxon-area cladograms were reduced using the conditions of Assumption 0 (Wiley 1987). To do this, the terms and components (Nelson 1979) of each taxon-area cladogram were scored in an area X term and component data matrix, with species presence in an area coded 1, and species absence coded 0 (Wiley 1987). The resultant fundamental area cladogram was rooted by designating an out-area coded by all 0's. Assumption 0 determines that widespread species indicate a monophyletic relationship for the areas they occupy. This set of conditions allows straightforward computation of a fundamental area cladogram, as it is determined as the most parsimonious rooted network of areas derivable from the area X term/component matrix. This network was obtained using the m* and bb* options of Hennig86.

The fundamental area cladograms for *Elliptoleus* and *Calathus* were compared by two methods. In the first, the areas unique to each taxon were removed from the fundamental area cladograms, and a consensus cladogram determined by the method of Adams (1972). Areas unique to either fundamental area cladogram were then replaced on the consensus cladogram based on their position in either fundamental area cladogram. By the second method (Wiley 1987), the area X term/component data matrices of the two genera were combined, with the areas missing from either taxon-area cladogram coded as unknown (? in Hennig86) for all terms and components. The combined data matrix was then analyzed using the m* and bb* options of Hennig86, producing a single set of most parsimonious area networks.

RESULTS

Taxon cladograms.—The exact analysis of *Elliptoleus* data results in four equally parsimonious cladograms of 31 steps, consistency index 0.64, and retention index 0.63 (Farris 1989). The taxon cladogram chosen for this analysis was one of the four (Fig. 3). The others differed by resolving *E. vixstriatus* as the sister group for the six other species joining at the trichotomy of Fig. 3 (2 trees), and by placing *E. zapotecorum* and *E. whiteheadi* as sister taxa (2 trees). The topology of Fig. 3 is preferred because it: 1) is one of the 4 most parsimonious cladograms, 2) does not resolve the trichotomy based on ambiguous data, and 3) places the geographically adjacent *E. crepericornis* and *E. whiteheadi* as sister species (Liebherr 1991).

Analysis of the *Calathus* data resulted in nine equally parsimonious cladograms of 30 steps, consistency index 0.46, and retention index 0.69. Of the nine, three cladograms satisfied a character transformation series whereby flight wing reduction was unreversed during phylogeny (Fig. 4). The six other cladograms necessitated that *C. advena,* or *C. advena* and *C. opaculus* evolve the macropterous condition from ancestors that were constantly brachypterous. This transformation series was rejected because of the single allelic control of wing polymorphism in several closely related carabids (Lindroth 1946, Aukema 1986), and the assumption that once flight wings were lost, selection would operate to break up the closely linked wing development genes, facilitating further reduction in the metathoracic sclerites associated with the flight musculature. This argument, then, can be characterized under Dollo's rule for the reduction of complex characters.

The three equally parsimonious *Calathus* cladograms differ in resolution of the six species comprising the sister group to *C. aztec* (Fig. 4). Successive sister groups totally resolved on one cladogram, and re-
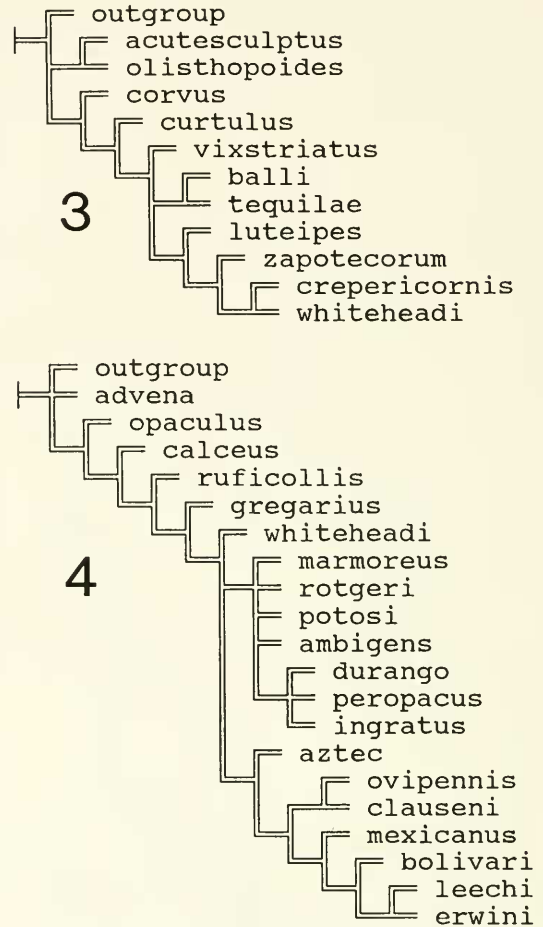
Figs. 3, 4. Taxon cladograms determined using Hennig86. 3, *Elliptoleus* species. 4, Nearctic *Calathus* species.

solved in part on one of the other two include: 1) *C. aztec,* 2) *C. ovipennis* + *C. clauseni,* 3) *C. mexicanus,* and 4) *C. bolivari* + *C. leechi* + *C. erwini* (Fig. 4). The two cladograms partially resolving these relationships include a trichotomy of the above groups 1, 2, and 3 + 4 while defining 3 as the sister group of 4; and a trichotomy of groups 2, 3, and 4 while defining group 1 as the sister of 2 + 3 + 4. As the three cladograms result in identical fundamental area cladograms under Assumption 0, choosing one over any other is of no further consequence for this analysis.
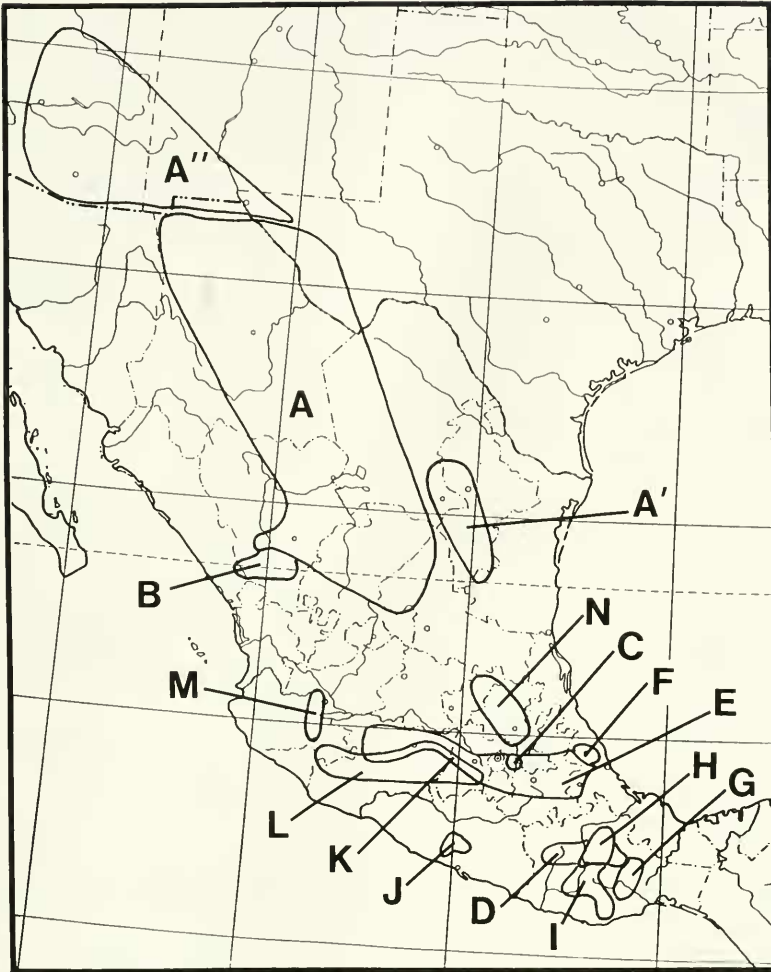
Fig. 5. Areas of endemism defined by the distributions of species of *Elliptoleus* and *Calathus.*

Taxon-area cladograms.—Areas of endemism were defined for each group, and were subsequently coordinated to allow comparison of area relationships between the two genera (Fig. 5). The taxon-area cladogram for *Elliptoleus* (Fig. 6) illustrates the relatively restricted distributions of most species in the genus. No more than two species are ever sympatric. *Elliptoleus vixstriatus* is the most widely distributed species, found throughout the eastern Transvolcanic Sierra. Other species are very restricted; e.g. *E. olisthopoides* ranging from southwestern Durango to eastern Sinaloa (area B), *E. corvus* found near Volcan Ixtaccihuatl (area C),

and *E. luteipes* distributed on the flanks of Cofre de Perote (area F). Areas of endemism in this genus are delimited by river valleys, or are associated with uplifted areas surrounding major volcanoes.

The taxon-area cladogram for *Calathus* (Fig. 7) clearly illustrates a sister relationship of the Mexican areas to North America north of Mexico; five successive cladistically basal branches represent North American species. *Calathus* species are more widely distributed than *Elliptoleus* species, and up to four species may be sympatric; e.g. in area C. Other species are of restricted distribution; e.g. *C. whiteheadi* found in area
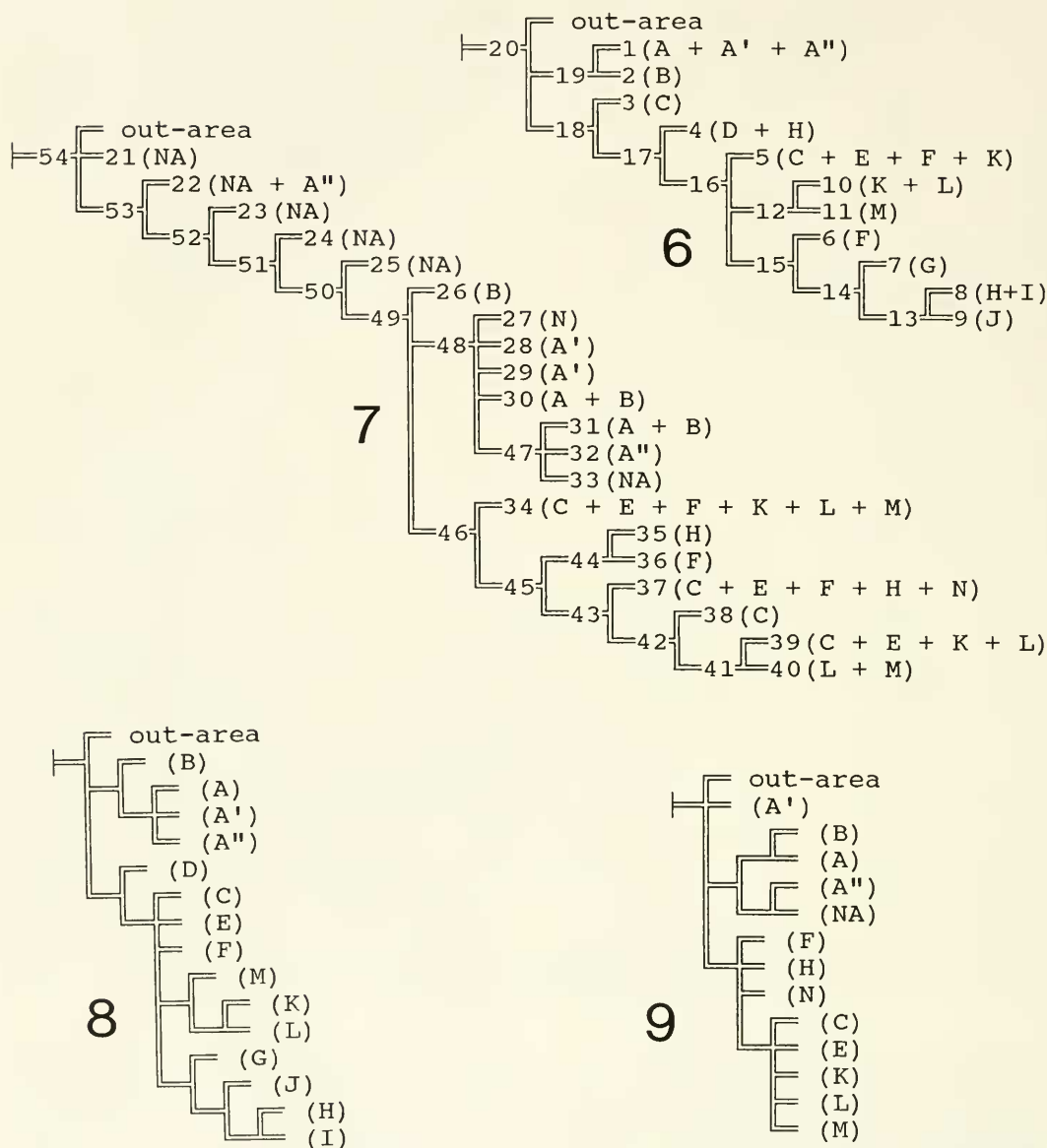
Figs. 6–9.   6, 7. Taxon-area cladograms derived from taxon cladograms. 6, cladogram based on *Elliptoleus* distributions. 7, cladogram based on *Calathus* distributions. Figs. 8, 9. Fundamental area cladograms derived via parsimony analysis from taxon-area cladograms. 8, consensus cladogram of five equally parsimonious fundamental area cladograms for areas occupied by *Elliptoleus*. 9, consensus cladogram of 11 equally parsimonious fundamental area cladograms for areas occupied by *Calathus*.

B, *C. bolivari* restricted to area C, and *C. clauseni* to area F. Whereas *E. acutesculptus* is widespread in Coahuila and Chihuahua (areas A, A′, and A″), three species of *Calathus* are restricted to portions of its range.

Several areas are represented by taxa in only one of the genera: areas D, G, I, and J by *Elliptoleus*; areas N and North American north of Mexico (NA) by *Calathus*.

Fundamental area cladograms.—The area X term/component data matrices for the two genera (Table 1) were scored for species

Table 1. Area × term and component data matrix for areas occupied by *Elliptoleus* and Nearctic *Calathus*. Term and component numbers correspond to Figures 6 and 7. Areas represented by components 50 to 54 are identical to those of component 49. As inclusion of these all-inclusive components does not affect the topology of any fundamental area cladogram, they are deleted from the matrix. If no taxon within the genus occurs in an area, that area is coded as unknown (?). Such coded areas are used only in the combined analysis method of Wiley (1987).

| | Term and Component | | | | | |
| | *Elliptoleus* | | | *Calathus* | | |
Area	123456789	1111111111 0123456789	2 0	222222222 123456789	3333333333 0123456789	4444444444 0123456789
out-area	000000000	0000000000	0	000000000	0000000000	0000000000
A	100000000	0000000001	1	000000000	1100000000	0000000111
A'	100000000	0000000001	1	000000011	0000000000	0000000011
A"	100000000	0000000001	1	010000000	0010000000	0000000111
B	010000000	0000000001	1	000001000	1100000000	0000000111
C	001010000	0000001110	1	000000000	0000100111	0111011001
D	000100000	0000000110	1	?????????	??????????	??????????
E	000010000	0000001110	1	000000000	0000100101	0111011001
F	000011000	0000011110	1	000000000	0000101100	0001111001
G	000000100	0000111110	1	?????????	??????????	??????????
H	000100010	0001111110	1	000000000	0000010100	0001111001
I	000000010	0001111110	1	?????????	??????????	??????????
J	000000001	0001111110	1	?????????	??????????	??????????
K	000010000	1010001110	1	000000000	0000100001	0111011001
L	000000000	1010001110	1	000000000	0000100001	1111011001
M	000000000	0110001110	1	000000000	0000100000	1111011001
N	?????????	??????????	?	000000100	0000000100	0001011011
NA	?????????	??????????	?	111110000	0001000000	0000000111

presence/absence using the term and component numbers of Figs. 6 and 7. Using Hennig86, five equally parsimonious fundamental area cladograms result for the analysis of *Elliptoleus*. The five area cladograms are similar—differing only in the relationships of areas C, E, and F—and can be summarized using a strict consensus cladogram (Fig. 8). The consensus cladogram exhibits a basal dichotomy between areas A, A', A", and B, and areas C to M. This sister area relationship corresponds to the Sierra Madre Occidental plus Sierra Madre Oriental being the sister area to the Transvolcanic Sierra plus Sierra Madre del Sur areas further south (Fig. 5). Other monophyletic sets of areas include areas G to J in the Sierra Madre del Sur, and areas K to M in the western Transvolcanic Sierra.

Analysis of the *Calathus* data results in 11 equally parsimonious fundamental area cladograms. These cladograms differ in the resolution of: 1) areas C, E, K, L, and M, 2) areas F, H, and N relative to the former, and 3) area A' as sister to areas A, A", B, plus NA, or as one lineage of a basal trichotomy on the cladogram. The strict consensus of the 11 cladograms (Fig. 9) preserves monophyly of the Transvolcanic Sierran areas C, E, K, L, and M. Areas A, A", and B form a monophyletic group including NA, with A' joining at a basal trichotomy.

General area cladogram.—For the consensus method of determining a general area cladogram, fundamental area cladograms including areas A to C, E, F, H, and K to M were derived (Figs. 10, 11). The Adams consensus of these two cladograms (Fig. 12) resolves two sister sets of areas; A, A', A", and B as one group, and C, E, F, H, K, L, and M as the second. This basal dichotomy
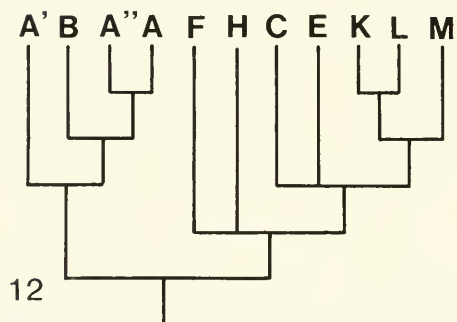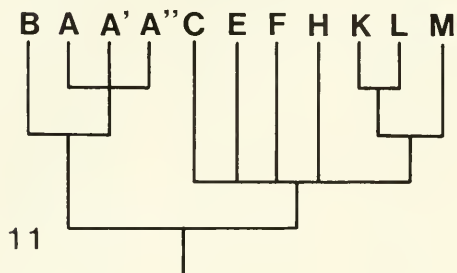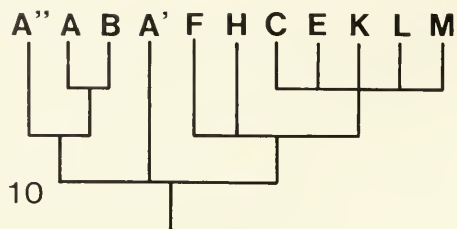
Figs. 10–12. Area cladograms including only areas occupied by species in both *Elliptoleus* and *Calathus*. 10, area cladogram based on *Calathus*. 11, area cladogram based on *Elliptoleus*. 12, Adams consensus cladogram of Figs. 10 and 11; a general area cladogram including areas occupied by taxa in both genera.

is represented in the *Elliptoleus* fundamental area cladogram (Fig. 8). Within the Transvolcanic Sierran areas, K, L, and M are defined monophyletically relative to areas C and E, with area F related at a lower level of cladistic relationship.

If areas uniquely occupied by either genus are replaced on this consensus cladogram (Fig. 13), the distributionally defined cladistic areas generally join, forming traditionally defined geographic regions or geological features. Resolution of the Sierra

Madre del Sur areas G to J and the Transvolcanic Sierran areas C, E, K, L, and M is supported. Area D, called the Old Oaxacan area, represents part of the distribution of *E. curtulus*, which is a cladistically basal species in that genus (Fig. 6). Separation of this area from areas G to J suggests a history whereby two cladistic lineages have occupied the Sierra Madre del Sur areas, an older relationship resulting in *E. curtulus*, and a younger relationship resulting in *E. whiteheadi*, *E. crepericornis*, and *E. zapotecorum*. Area F, the uplifted areas surrounding Cofre de Perote, is separated from the other Transvolcanic Sierran areas, suggesting earlier vicariance at the eastern end of the Transvolcanic Sierran region relative to the western portions.

The basal dichotomy of the Sierra Madre Occidental areas and areas of the Transvolcanic Sierra and Sierra Madre del Sur is supported in the consensus cladogram. The cladistic position of *C. ingratus* at a trichotomy with *C. peropacus* and *C. durango*, and the widespread distribution of *C. opaculus* in areas A″ and NA (Figs. 4, 7), results in area NA being considered the sister to A″. This occurs in spite of *Calathus* exhibiting a cladistically basal sister area relationship between the Mexican and Arizonan areas (areas A to N), and North America north of Mexico; i.e. the Nearctic Distribution Pattern (Fig. 7). As this result is due to the taxon-area cladogram coding procedure under Assumption 0, I explain the placement of area "na" within the northern Mexican areas as a consequence of secondary dispersal, and suggest that an older relationship between North America north of Mexico (area NA) and Mexico proper should also be recognized.

This analysis separates the two areas that comprise the Sierra Madre Oriental. Area A′, or the northern Sierra Madre Oriental, exhibits affinities to the Sierra Madre Occidental, and area N, or the southern Sierra Madre Oriental, is grouped with the areas to the south. This result occurs because of
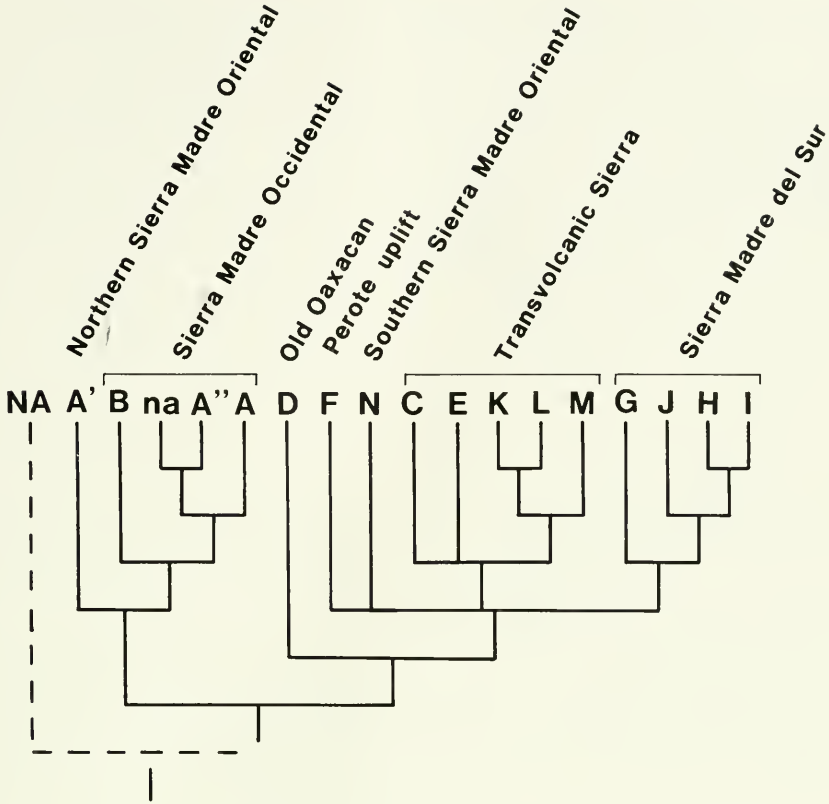
Fig. 13. General area cladogram derived by adding areas unique to either genus to Fig. 12, given the area relationships of Figs. 8 and 9. Area na's relationships were determined by parsimony analysis, but interpreted as due to secondary dispersal in favor of a basal vicariant sister area relationship of NA with Mexican areas (see text).

the undue influence of widespread taxa in determining area relationships under Assumption 0. In this case, the widely distributed *C. mexicanus* inhabits area N and areas of the Transvolcanic Sierra (Figs. 4, 7), causing area N to exhibit southern affinities. This results even though *C. marmoreus*, a species endemic to the southern Sierra Madre Oriental (Figs. 4, 7) is cladistically related to species in the Sierra Madre Occidental. Once again, we could hypothesize a recent secondary dispersal of *C. mexicanus* into area N from the south, and an older relationship of the entire Sierra Madre Oriental with the Sierra Madre Occidental areas to the west.

The general area cladogram derived via the consensus method can be portrayed geographically by plotting the levels of cladistic relationship on a map of Mexico (Fig. 14). The resulting "mola" map illustrates a decrease in the size of areas of endemism from north to south. The southern areas of the Sierra Madre del Sur are connected to the Transvolcanic Sierran areas at a relatively low level of relationship. Based on current geologic structures, historically this connection has been made along the Atlantic versant via the Sierra de Oaxaca. The Rio Balsas depression need not have been traversed by any taxa in *Calathus* or *Elliptoleus* during their history. The larger northern areas are related to the southern areas at only a low level of cladistic relationship, indicating a relatively long period for the isolation and differentiation of taxa in the Transvolcanic Sierra and Sierra Madre del Sur.

Fig. 14. General area cladogram represented geographically as a "mola" map, with contours including progressively more taxa at progressively lower levels of cladistic relationship.
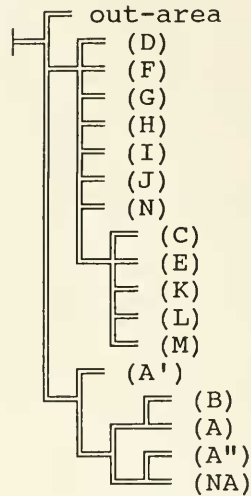

Fig. 15. General area cladogram derived by cladistic parsimony based on combined data matrix for *Ellipotoleus* and *Calathus.* Cladogram is consensus of 24 equally parsimonious cladograms.

If the data matrices derived from the two taxon-area cladograms are analyzed in combination (Table 1) using the method of Wiley (1987), ambiguity introduced by missing areas in the two genera results in 24 equally parsimonious general area cladograms produced by Hennig86. The consensus tree of these 24 cladograms (Fig. 15) exhibits an extensive lack of resolution. Nonetheless, the basal dichotomy between the Sierra Madre Occidental areas and the areas to the south is supported, as is monophyly of the Transvolcanic Sierran areas C, E, K, L, and M. Within the Sierra Madre Occidental areas, area A' is again placed as the outgroup to the others (Figs. 13, 15), and areas A" and NA are sisters.

DISCUSSION

Taxon-area relationships in *Calathus* and *Elliptoleus* are congruent, even though species in these genera exhibit very different seasonality patterns. *Elliptoleus* species would appear to spend the winter as adults, as teneral individuals have been collected in August (Liebherr 1991). In support of this contention, adults have been collected in low numbers in January, February, and March, although the relative rarity of specimens precludes certainty about any aspect of *Elliptoleus* life history. All species of *Calathus,* conversely, overwinter in the larval stage (Gilbert 1956, Hůrka 1986). That vicariant patterns in these two genera are congruent suggests that individuals of these species are tightly tied to particular habitat types, with vicariance fragmenting particular portions of these habitats. Whether larvae or adults are present during drier, wetter, cooler, or warmer seasons would not appear important in determining the operation of vicariant barriers. This interpretation discounts any dispersive activities of individuals as causative forces in the zoogeographic history of these groups, an interpretation consistent with the extremely low vagility of these beetles.

This analysis assumes adherence to cladistic parsimony for the establishment of taxon cladograms. Ball and Negre (1972)

proposed a significantly different cladogram and attendant zoogeographic scenario for *Calathus*. They hypothesized several invasions of North America by lineages of *Calathus* originating in the Old World, and three invasions of Mexico from North America. Whereas their hypothesis is possible, the cladogram they base it on is considerably more complex than the one proposed above; the cladogram of Ball and Negre is 36 steps long, whereas the cladogram herein is 30 steps long. In this case, then, a more parsimonious cladogram for *Calathus* results in concordant patterns with *Elliptoleus,* whereas Ball and Negre's more complex cladogram does not. Acceptance of the more parsimonious cladogram is therefore supported by both within-taxon and between-taxon parsimony criteria.

The pattern of area relationships set out above may be predicted for other taxa that are ecologically restricted to humid montane forest habitats, and who have sister groups inhabiting North America north of Mexico. One such group is composed of the sister genera *Viridimicus* and *Parabyrsopolis* of the scarab beetle tribe Rutelini, subfamily Rutelinae (Jameson 1990). *Parabyrsopolis* is monotypic, with its single species, *P. chihuahuae,* restricted to pine-oak forests in the Sierra Madre Occidental and western Transvolcanic Sierra (areas A, B, K, L, and M). *Viridimicus* comprises six species, two of which are found southeast of the Isthmus of Tehuantepec, one whose range is unknown, and three others: *V. ratcliffei* found in area F, *V. impunctatus* restricted to area J, and *V. cyanochlorus* occurring in area I. These two genera have the North American genus *Paracotalpa* and the northern to central Mexican genus *Parachrysina* as unresolved outgroups. The cladogram proposed by Jameson for the taxa of *Parabyrsopolis* and *Viridimicus,* including only those taxa inhabiting areas discussed for *Calathus* and *Elliptoleus,* defines an area cladogram of the topology: (A + B + K + L + M (F (I + J))). This cladogram exhibits a basal dichotomy of the Sierra Madre Occidental plus western Transvolcanic Sierra, versus the eastern Transvolcanic Sierra plus Sierra Madre del Sur. Whereas this basal structure differs from the general area cladogram developed from *Calathus* and *Elliptoleus,* the relationship of areas K, L, and M with A and B is based strictly on the widespread distribution of *P. chihuahuae.* The closer relationship of Sierra Madre del Sur areas (I and J) relative to area F of the Transvolcanic Sierra is shared with the general area cladogram based on the carabid taxa. The scarab taxon-area cladogram supports the Rio Balsas depression as a potent biogeographic barrier, as the Sierra Madre del Sur taxa are related to those further north via taxa in the eastern Transvolcanic Sierra, i.e. the Atlantic versant in Veracruz and Oaxaca. That two of the species of *Viridimicus* inhabit the Sierra Madre de Chiapas, and that the *Parachrysina* outgroup occurs in central to northern Mexico, suggests that these beetles may disperse more readily than *Calathus* or *Elliptoleus,* or that their ecological requirements are different, possibly explaining the discrepancies in patterns among the groups.

Other taxa exhibit elements of the area relationships outlined for *Calathus* and *Elliptoleus.* The scarab beetle genus *Geotrupes* includes 12 Mexican and Central American species, distributed in montane regions from the Sierra Madre de Chiapas to the Sierra Madre Occidental (Howden 1966). The Middle American species are more closely related to Old World taxa than they are to the species in eastern North America. A taxon-area cladogram of the Middle American species could provide illuminating comparison with any of the above-mentioned taxa.

The monophyletic cyprinid fish genus *Algansea,* found in the western Transvolcanic Sierra and northward flowing rivers, forms the sister group to five species of the genus *Gila,* distributed further north in the Sierra Madre Occidental (Barbour and Miller 1978). Other fish taxa, including *Yuyuria,*

Salmo, and *Catastomus* exhibit similar relationships, and are considered representative of a Western Mountain Track by Miller and Smith (1986). The distribution of this track comprises a subset of the areas included in Halffter's Nearctic Distribution Pattern.

Some ambiguity exists in the present analysis concerning the relationships of the areas in the Sierra Madre Oriental, and whether the Sierra Madre Oriental should be considered a monophyletic set of areas. That the northern portions of this range share faunal elements with the Sierra Madre Occidental is well established. A number of lizard (Martin 1958) and mammal (Baker 1956) species of the highland areas of southern Coahuila, Nuevo Leon, and Tamaulipas are also found in the Sierra Madre Occidental. In other cases, divergence at the subspecific or specific level is observed between taxa in the eastern and western mountains, with sister-group status between the taxa presumed, though not established cladistically. Much more mesic conditions in the Chihuahuan desert during the Pleistocene (Arellano 1951, Van Devender and Burgess 1985) and before would have facilitated such biotic interchange. The affinities of the southern reaches of the mountain system are mixed. Affinities to the south are suggested by the widespread distribution of *C. mexicanus* (Figs. 4, 7). Affinities to the north are supported by the placement of *C. marmoreus* with other species in areas A, A', A″, B, and NA (Figs. 4, 5, 7). Discovery of *Elliptoleus* populations in area N would provide another test of whether area N's principal affinities lie to the north or to the south.

Assumption 0 was used to derive fundamental area cladograms in this analysis because of the several widespread taxa in both genera. Use of Assumptions 1 and 2 result in so many possible fundamental area cladograms for each genus that we cannot currently complete the analysis (JKL, unpubl. data). In the future, given greater computing power, the search for congruence among fundamental area cladograms determined under Assumptions 1 or 2 conditions may reduce the possible set of general area cladograms to a manageable number. At the present time, congruence under Assumption 0 establishes a general hypothesis for further testing.

The use of a consensus cladogram (Figs. 12, 13) for the comparison of fundamental area cladograms provides much greater resolution than the combined matrix parsimony analysis with missing areas coded as unknowns (Fig. 15). This suggests that whenever there are areas missing from one or another taxon's distribution, the analysis of combined data matrices should be avoided when deriving a general area cladogram. Moreover, the use of Adams' consensus method allows resolution of areas based on resolution observed in only one of the fundamental area cladograms, resulting in a more falsifiable general hypothesis.

DEDICATION

It is no coincidence that patronymical species names honoring Don Whitehead occur in the genera *Calathus* and *Elliptoleus.* Don, in collaboration with George Ball, contributed vast numbers of specimens of undescribed taxa to the Strickland Museum of Entomology, University of Alberta. This collection will continue to form a legacy that will allow us to gain an understanding of the Mexican montane insect fauna and the areas it occupies. Indeed, the recently published description of *Viridimicus cyanochlorus* includes a "Ball-Whitehead" holotype specimen (Jameson 1990). Don also pioneered the modern revision of the Mexican *Platynus,* making it much easier for all of us who will follow. Don will remain a character in the unfolding story of the Mexican biota, even as many of the areas he collected become ecologically decimated. May understanding the area relationships in Mexico assist efforts to assess their im-

portance, hopefully assisting their preservation.

LITERATURE CITED

Adams, E. N., III. 1972. Consensus techniques and the comparison of taxonomic trees. Systematic Zoology 21: 390–397.

Arellano, A. R. V. 1951. Research on the continental Neogene of Mexico. American Journal of Science 249: 604–616.

Aukema, B. 1986. Winglength determination in relation to dispersal by flight in two wing dimorphic species of Calathus Bonelli (Coleoptera, Carabidae), pp. 91–99. In den Boer, P. J., M. L. Luff, D. Mossakowski, and F. Weber, eds., Carabid Beetles, Their Adaptations and Dynamics. G. Fischer, Stuttgart.

Baker, R. H. 1956. Mammals of Coahuila, Mexico. University of Kansas Publications, Museum of Natural History 9: 125–335.

Ball, G. E. and J. Negre. 1972. The taxonomy of the Nearctic species of the genus Calathus Bonelli (Coleoptera: Carabidae: Agonini). Transactions of the Entomological Society of America 98: 412–533.

Barbour, C. D. and R. R. Miller. 1978. A revision of the Mexican cyprinid fish genus Algansea. Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 155, 72 pp.

Carpenter, J. M. In press. Biogeographic patterns in the Vespidae (Hymenoptera): Two views of Africa and South America. Annals of the Missouri Botanical Garden

Farris, J. S. 1988. Hennig, Hennig86 reference, version 1.5 (a cladistics computer program available from the author at 41 Admiral St., Port Jefferson Station, New York 11776).

———. 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

Gilbert, O. 1956. The natural histories of four species of Calathus (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales. Oikos 7: 22–47.

Halffter, G. 1976. Distribucion de los insectos en la zona de transicion Mexicana. Relaciones con la entomofauna de Norteamerica. Folia Entomologica Mexicana, No. 35, 64 pp.

———. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review of Entomology 32: 95–114.

Howden, H. F. 1966. Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae (Coleoptera). Canadian Entomologist 98: 1177–1190.

Humphries, C. J. and L. Parenti. 1986. Cladistic Biogeography. Clarendon Press, Oxford.

Hůrka, K. 1986. The developmental type of Carabidae in the temperate zone as a taxonomic character, pp. 187–193. In den Boer, P. J., M. L. Luff, D. Mossakowski, and F. Weber, eds., Carabid Beetles, Their Adaptations and Dynamics. G. Fischer, Stuttgart.

Jameson, M. L. 1990. Revision, phylogeny and biogeography of the genera Parabyrsopolis Ohaus and Viridimicus, new genus (Coleoptera: Scarabaeidae: Rutelinae). Coleopterists Bulletin 44: 377–422.

Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18: 1–32.

Liebherr, J. K. 1991. Revision and phylogeny of the Anchomenus clade: The genera Tetraleucus, Anchomenus, Sericoda, and Elliptoleus (Coleoptera: Carabidae: Platynini). Bulletin of the American Museum of Natural History 202: 1–167.

Lindroth, C. H. 1946. Inheritance of wing polymorphism in Pterostichus anthracinus Ill. Hereditas 32: 37–40.

Martin, P. S. 1958. A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Miscellaneous Publication of the Museum of Zoology, University of Michigan, No. 101, 102 pp.

Miller, R. R. and M. L. Smith. 1986. Origin and geography of the fishes of Central Mexico, pp. 487–517. In Hocutt, C. H. and E. O. Wiley, eds., The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York.

Nelson, G. H. 1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's Famille de Plantes (1763–1764). Systematic Zoology 28: 1–21.

Nelson, G. H. and N. I. Platnick. 1981. Systematics and Biogeography, Cladistics and Vicariance. Columbia Univ. Press, New York.

Page, R. D. M. 1989. Component User's Manual, release 1.5. Auckland, New Zealand.

———. 1990. Component analysis: A valiant failure? Cladistics 6: 119–136.

Platnick, N. I. and G. H. Nelson. 1978. A method of analysis for historical biogeography. Systematic Zoology 27: 1–16.

Van Devender, T. R. and T. L. Burgess. 1985. Late

Pleistocene woodlands in the Bolson de Mapimi: A refugium for the Chihuahuan desert biota? Quaternary Research 24: 346–353.

Whitehead, D. R. 1973. Annotated key to *Platynus,* including *Mexisphodrus* and most "*Colpodes,*" so far described from North American including Mexico (Coleoptera: Carabidae: Agonini). Quaestiones Entomologicae 9: 173–217.

Wiley, E. O. 1987. Methods in vicariance biogeography, pp. 283–306. *In* Hovenkamp, P., ed., Systematics and Evolution: A Matter of Diversity. Institute of Systematic Botany, Utrecht University.

Zandee, M. and M. C. Roos. 1987. Component-compatibility in historical biogeography. Cladistics 3: 305–332.